

A REVISION OF THE FAMILIES SYNNEURIDAE AND CANTHYLOSCELIDAE (DIPTERA)

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SYNOPSIS

The families Synneuridae and Canthyloscelidae (in recent years combined under the single name Hyperoscelidae) are revised. A new genus and species, *Exiliscelis californiensis*, is described from North America and assigned to the Synneuridae. *Synneuron decipiens* and *Canthyloscelis balaena* are new species described from North America and New Zealand respectively. New synonymy is proposed in the genera *Hyperoscelis* and *Canthyloscelis*. Twelve species are recognized in the families and keys are provided for the identification of all known species. The phylogeny of the group and its relationships with Scatopsidae are discussed and a systematic analysis is presented to show these relationships. This is related to the existing knowledge of the immature stages.

INTRODUCTION

In preparing the description of a new genus and species to be included in the family Hyperoscelidae it was apparent that although the group has been the subject of what might be regarded as an inordinate amount of attention in recent years, especially in view of the few species contained in it, there was the need for a further review, including a change in the family name. The reasons for this review are that (a) the new genus required the recharacterization of the classification of the group; (b) a number of previous identifications were incorrect and had confused the distribution patterns of species; (c) these misidentifications resulted in synonymy in *Hyperoscelis* and *Canthyloscelis* and in the description of new species in *Synneuron* and *Canthyloscelis*; (d) some further comment on the affinities of the group was appropriate. This revision is thus a compilation of the data published under the family name Hyperoscelidae, with additional data that have become available through the examination of material from almost every known record of the group, in the light of the discovery of a new genus in North America. This small widespread group of flies presents interesting material for the study of phylogeny and zoogeography.

MATERIAL

Specimens of *Canthyloscelis* are well represented in the British Museum (Natural History) (BMNH); extra material of this and material of other genera has been examined by gifts and loans from the following.

CNC, Ottawa	Canadian National Collection, Ottawa, Canada (Dr B. V. Peterson)
DEFW, St Paul	Department of Entomology, Fisheries and Wildlife, University of Minnesota, St Paul, Minnesota, U.S.A. (Dr E. F. Cook)
IAEME, Moscow	Institute of Animal Evolutionary Morphology and Ecology, Moscow, U.S.S.R. (Dr B. M. Mamaev)
IRSNB, Brussels	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (the late Dr J. Verbeke)
KUF, Fukuoka	Kyushu University, Fukuoka, Japan (Dr H. Shima)
J. Martinovsky	Kosmonautu, Olomouc, Czechoslovakia (private collection)
NM, Vienna	Naturhistorisches Museum, Vienna, Austria (Dr R. Lichtenberg)
NR, Stockholm	Naturhistoriska Riksmuseet, Stockholm, Sweden (Dr P. I. Persson)
USNM, Washington	U.S. National Museum, Washington, D.C., U.S.A. (Dr R. Gagné)
ZMU, Helsinki	Zoological Museum of the University, Helsinki, Finland (Dr B. Lindeberg)

HISTORICAL REVIEW

The three genera *Corynoscelis* (= *Hyperoscelis*), *Synneuron* and *Canthyloscelis* were all described as related to *Scatopse*, and Edwards (*in* Tonnoir, 1927b) brought them together as the subfamily Corynoscelinae, although he had reservations about including them in the Scatopsidae. Enderlein (1912) gave *Corynoscelis* subfamily rank in the Scatopsidae and later (1936) considered each of *Corynoscelis*, *Synneuron* and *Ectactia* Enderlein as subfamilies of the new family Corynoscelidae. He did not mention *Canthyloscelis*, but he may have considered this New Zealand genus

outside the scope of his work. Rodendorf (1938), in discussing some Mesozoic Diptera, similarly referred to the Corynoscelidae and later (1951; translated into German, 1958-59), in discussing the locomotory organs of Diptera, separated the Synneuronidae and Canthyloscelididae (which included '*Corynoscelis*'). Hennig, in such papers as his discussion on wing venation in Diptera (1954) and in his use of this group to demonstrate potential origins of Australasian/South American faunal relationships (1960), referred to the Corynoscelidae, but in this latter discussion he was inclined to ignore *Synneuron* as possibly not belonging to the same family. Tollet (1959), although apparently aware of Enderlein's work, but possibly not aware of the other work, described Corynoscelidae as a supposedly new family with two supposedly new subfamilies: Synneurinae and Corynoscelinae. *Canthyloscelis* was included in the Corynoscelinae, but he did not discuss *Ectaetia*. Hardy & Nagatomi (1960), having been informed of the homonymy of *Corynoscelis* Boheman, 1858 with *Corynoscelis* Burmeister, 1847, renamed the genus *Hyperoscelis* and hence the family Hyperoscelidae. Cook (1963) did not separate the family into subfamilies. Rodendorf (1964; translated into English, 1974) split the group into two families Synneurontidae and Hyperoscelididae. The translation into English of Hennig's (1960) paper (1965) referred to Hyperoscelidae. Mamaev & Krivosheina (e.g. 1969) referred to the Synneurontinae and Hyperoscelidinae. Thus there is a lot of difference of opinion about the higher classification of the group, that of the majority being that the three genera be combined into a single family, with *Synneuron* as a separate subfamily from the other two genera. It should be noted that *Ectaetia* is considered to belong in the Scatopsidae and is outside the scope of the present work.

It will also be obvious from the above that authors have been confused about the 'correct' family-group name endings required for these genera: *Corynoscelis*, *Canthyloscelis* and *Hyperoscelis* have given rise to the family-group endings -scelidae, and -scelididae, while *Synneuron* has given rise to Synneuridae, Synneuronidae and Synneurontidae. Steyskal (1972) has gone to some lengths to discuss the question of -scelis-like endings, and my impression from this is that *Canthyloscelis*, etc., should produce the family name Canthyloscelidae (like his example *Glyptoscelis*). This whole question is remote from science and is beyond the knowledge of an ever increasing proportion of zoologists. In nearly all generic names in Zoology, the grammatically correct family-group name is formed in one of two ways: (a) if the name ends in a vowel, this is replaced by *idae*; (b) if the name ends in a consonant, then this and its preceding vowel are replaced by *idae*. I have applied this system to the names *Synneuron* and *Canthyloscelis* to give the family names Synneuridae and Canthyloscelidae, at least one of which I believe to be grammatically correct.

A fourth genus is now available for a single species from California and Oregon in the United States of America. This genus is described below with notes and keys to the species of the other genera, a discussion on the relationships within the four genera and with related families, followed by a world checklist.

From my investigations of the morphology and in an attempt to maintain some stability whilst observing the rules of the *International Code of Zoological Nomenclature*, I am regarding the group as consisting of two families which are

closely related to the Scatopsidae. However, it must be admitted that features of the early stages do not support this division (see p. 95).

In the adults the three families Scatopsidae, Synneuridae and Canthyloscelidae collectively differ from other families of Nematocera by the following combination of characters.

Holoptic (or almost so). Eyes hairy. Ocelli present. Proboscis large with obvious labellae. Mesonotal phragma well developed and invading abdomen. Wings with vein *Sc* absent or ending free, R_1 not extending far beyond middle of wing (usually shorter), R_{2+3} absent, no discal cell, single anal vein present or absent. At most seven unmodified pregenital segments in both sexes. Laterites present on each abdominal segment between tergite and sternite. Males with well developed sperm pump either closely attached to genital complex or (Scatopsinae) lying free in abdomen and connecting via an elongate ejaculatory duct. External genitalia compact, without complex clasping apparatus.

These three families can be separated by the following key.

DIAGNOSTIC KEY TO THE FAMILIES SCATOPSIDAE,
SYNNEURIDAE AND CANTHYLOSCELIDAE

- 1 Median ocellus usually well-developed. Palpi 1-segmented. Antennae 7- to 12-segmented. Wings short and broad with well developed anal lobe. Posterior wing veins weak. Costa ending at R_5 . Vein R_4 absent. Vein *r-m* absent (an analogous vein sometimes present). Vein *m-cu* absent. Anal vein present or absent. Anterior spiracle on or partly or entirely separated from anepisternite.
Hind femur slender. Small, stout, black or black and yellow species
- SCATOPSIDAE**
- Median ocellus small or absent. Palpi 4-segmented. Antennae 12- or 16-segmented. Wings long and narrow without anal lobe. Posterior wing veins strongly developed, often well pigmented. Costa extending beyond R_5 . Vein R_4 present or R_1 and R_{4+5} fused. Vein *r-m* represented by a fusion. Vein *m-cu* present or represented by a fusion 2
- 2 Anal vein absent or present as a weak basal stump. Anterior spiracle at least partly separated from anepisternite. Hind femur slender. Small (wing-length: 2.5–5.0 mm), slender, black species **SYNNEURIDAE** (p. 70)
- Anal vein present. Anterior spiracle quite distinctly on anepisternite. Hind femur club-shaped. Larger (wing-length: 4.5–9.0 mm), robust, variegated species
CANTHYLOSCELIDAE (p. 77)

SYNNEURIDAE Enderlein

Synneurinae Enderlein, 1936 : 56. Type-genus: *Synneuron* Lundström, 1910.
Synneurionidae Enderlein; Rodendorf, 1951 : 64.
Synneurinae Enderlein; Tollet, 1959 : 144.
Synneurontidae Enderlein; Rodendorf, 1964 : 16.
Synneurontinae Enderlein; Mamaev & Krivosheina, 1969 : 933.
Synneurinae Enderlein; Martinovsky, 1972 : 353.

DIAGNOSIS. See above key.

DISTRIBUTION. Holarctic.

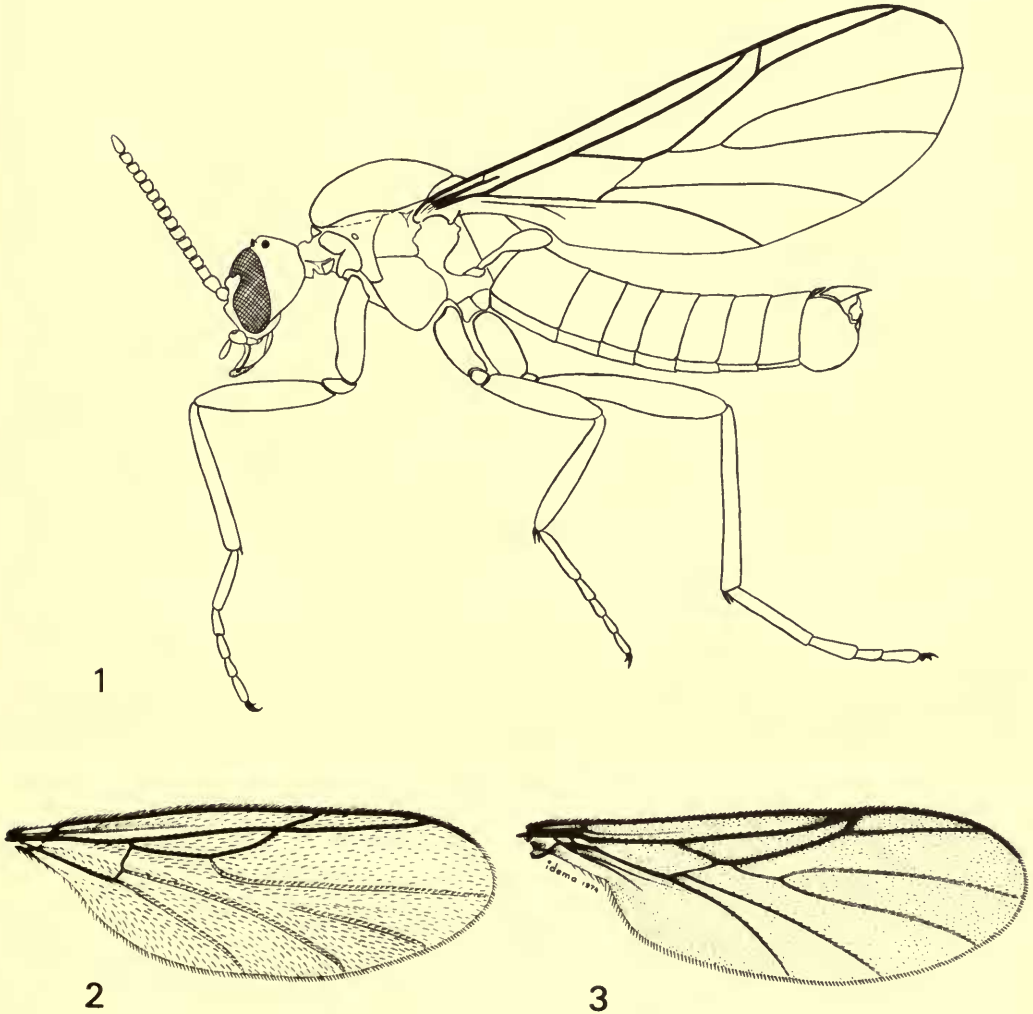
KEY TO GENERA

- 1 Anal vein present as faint trace at base. Antennae 16-segmented. Wing with R_s free from R_1 , vein R_4 present and ending in costa. Median fork complete. ♂ genitalia with prominent claspers. Ovipositor 2-segmented. (Nearctic)

EXILISCELIS (p. 75)

- Anal vein absent. Antennae 12-segmented. Wing with R_{4+5} fused with R_1 for short distance. Vein R_4 absent. Median fork with vein M_2 interrupted at base. ♂ genitalia without prominent claspers. Ovipositor 1-segmented. (Holarctic)

SYNNEURON (p. 72)



FIGS 1-3. 1, *Exiliscelis californiensis*, ♂. 2, *Synneuron decipiens*, wing. 3, *Exiliscelis californiensis*, wing. (Figs 2 & 3 by kind permission of the artist, R. Idema, 1974.)

SYNNEURON Lundström

(Text-figs 2, 9-12)

Synneuron Lundström, 1910 : 5. Type-species: *Synneuron annulipes* Lundström, 1910, by monotypy.

DIAGNOSIS. 3 ocelli, median one quite large. Antennae short, 12-segmented, the segments closely applied to each other. Palpi 4-segmented, last three segments short and round. Gena narrow, bottom of eyes very close to mouth margin. Proboscis prominent. Eyes broadly in contact above antennae, narrowly separated below. Meron reduced. Anterior spiracle not on main body of anepisternite. Fore tibia with single minute spur, other tibiae with a pair of minute spurs. Tarsal claws simple. Empodium small and narrow but with a fringe of long hairs. Hind femur not particularly swollen. Hind tibiae straight. Base of tibia and tarsal segments 1-4 usually whitened. Wings (Text-fig. 2) with posterior veins well developed but unpigmented. R_1 and R_s fused for a short distance before either reaches costa. Vein $r-m$ represented by a long fusion. M_2 interrupted at base. Cu_2 absent. Anal vein absent. Male abdomen with seven unmodified pregenital segments. Sperm pump relatively simple. Female abdomen with seven unmodified pregenital segments, ovipositor 1-segmented, single spermatheca.

DISCUSSION. *Synneuron* was known from the original single specimen from Finland and a second specimen (Duda, 1929; Frey, 1930) from this same country until Cook (1963) recorded several specimens from North America as the same species. Mamaev & Krivosheina (1969) were able to distinguish two species from adults bred from three samples of larvae found in rotting wood of birch, spruce and aspen. The material I have seen from North America is not *annulipes*. I have not seen specimens of *silvestre* Mamaev & Krivosheina, but believe it likely that the Nearctic material is not this species: although I do not find the venational characters given in the key by Mamaev & Krivosheina (1969) satisfactory (they do not even agree with their figures), *silvestre* is stated to be twice as large as *annulipes*, while the Nearctic material is the same size, and the description of the genitalia of *silvestre* does not seem to agree. I am therefore considering the Nearctic material as a new species.

KEY TO SPECIES OF *Synneuron*

(Note. I have not been able to include *silvestre* in a key to species (see p. 74), so the following key is to distinguish only *annulipes* and *decipiens*.)

The character of the leg colour is not very reliable and is only meant to imply that there is a greater tendency for North American specimens to have entirely dark legs and a greater tendency for Palaearctic specimens to have part of the tibia and tarsi distinctly white.)

- 1 Base of tibia and first four tarsal segments usually distinctly white (see note above).
 ♂ apodemes broadly bilobed basally and without prominent lateral apical lobes.
 Median process of apodeme broad and tongue-like, broadest toward tip. Gonocoxites small (Text-fig. 9) (Palaearctic) ***annulipes*** (p. 73)
- Base of tibia and first four tarsal segments usually somewhat whitened. ♂ apodemes rather rectangular basally with prominent apical lateral lobes. Median process of apodemes narrowing toward tip. Gonocoxite long, reaching beyond tergite 8 and with a reflexed apical lobe (Text-fig. 10) (Nearctic) ***decipiens*** (p. 73)

Synneuron annulipes Lundström

(Text-figs 9, 11)

Synneuron annulipes Lundström, 1910 : 6. Holotype ♀, FINLAND: Tuovilanlaks, 4.vii.1865 (*C. Lundström*) (ZMU, Helsinki) [examined].

DIAGNOSIS. As for genus. Genitalia as in Text-figs 9, 11. In the male the apodemes are bilobed basally and without prominent lateral apical lobes. Median process of apodeme broad and tongue-like, broadest towards the tip. Gonocoxites small. ♀ (only one specimen dissected) with tergite 8 more pronounced, sternite 8 less rounded laterally, cerci small. Spermatheca ovoid.

MATERIAL EXAMINED

Holotype ♀, FINLAND (details in synonymy).

FINLAND: Malla (*R. Frey*), 1 ♂ (ZMU, Helsinki); Utsjoki, Li., 18.viii.1948 (*E. Thuneberg*), 1 ♂ (ZMU, Helsinki); Kantalaks, Hellen, 1 ♀ (ZMU, Helsinki).

DISCUSSION. The only other specimens known so far are those reared from light-coloured mould under the bark of an aspen log in the Solnechnogorsk District, Moscow Region, U.S.S.R., by Mamaev & Krivosheina (1969). In the same paper they refer to further specimens, which may be this species, from a spruce stump in the Rybinsk District, Yaroslavl Province.

DISTRIBUTION. Finland, U.S.S.R. (Moscow Region).

Synneuron decipiens sp. n.

(Text-figs 2, 10, 12)

DIAGNOSIS. Wing (Text-fig. 2) 2.5-3.5 mm long. As *annulipes*, but differing in the structure of the genitalia. In the ♂ (Text-fig. 10) the apodemes are rather rectangular basally with prominent apical lateral lobes. The median process of the apodeme narrows toward its tip. The gonocoxites are long, reaching beyond the bilobed tergite 8 and with a reflexed apical lobe. ♀ (Text-fig. 12) with tergite 8 square-ended, sternite eight more evenly rounded laterally, cerci large and prominent. Spermatheca rounded.

MATERIAL EXAMINED.

Holotype ♂, CANADA: Quebec, Laniel, Cage 4, 15.vii.1934 (CNC, Ottawa).

Paratypes. CANADA: Quebec, Laniel, Cage 4, 29.vi.1934, 1 ♀ (BMNH); Quebec, Laniel, Cage 76, 1.viii.1934, 1 ♀ (CNC, Ottawa); Yukon Territory, North Fork Crossing, Mi 43, Peel Plt. Rd, 3500', 3.vii.1962 (*R. E. Leech*), 1 ♀ (CNC, Ottawa); British Columbia, Summit Lake, Mi 392, Alaska Hwy, 4500', 2-4.vii.1959 (*R. E. Leech*), 1 ♂ (CNC, Ottawa); Alberta, Johnston Canyon, Banff, 4700', 18.vii.1962 (*W. R. M. Mason*), 1 ♂ (BMNH); Saskatchewan, St. Victor, 49° 20' N 105° 54' W, 27.vi.1955 (*J. R. Vockeroth*), 1 ♂ (CNC, Ottawa); U.S.A.: Alaska, Matanuska, 7.vi.1945 (*J. C. Chamberlin*), 1 ♀ (CNC, Ottawa); Washington, Mt Rainier, Eagle Park, 19.vii.1922 (*A. L. Melander*), 1 ♂ (DEFW, St Paul); Colorado, Nederland, 300', 5.vii.1961 (*J. G. Chillcott*), 1 ♂ (CNC, Ottawa).

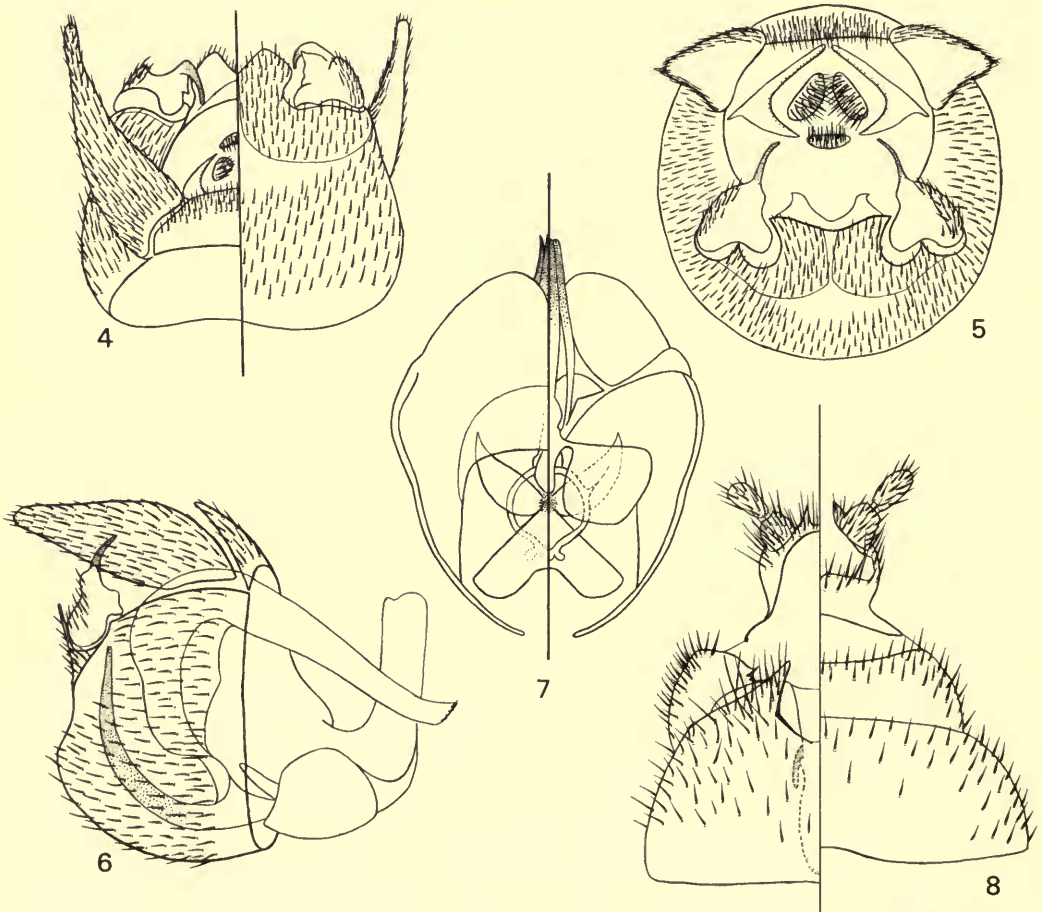
DISTRIBUTION. Northern North America.

Synneuron silvestre Mamaev & Krivosheina

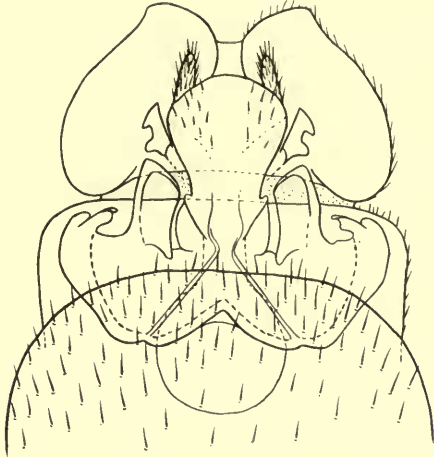
Synneuron silvestre Mamaev & Krivosheina, 1969 : 938. Holotype ♂, U.S.S.R.: Tula Province, Tula abatis, wood of rotten Birch, 5.v.1958 (B. M. Mamaev) (IAEME, Moscow) [not examined].

DISCUSSION. The type-series consisted of the holotype and 3 ♂ and 12 ♀ paratypes with the same data. No other specimens of this species are known. The species was not examined in the present study, but is stated to be twice as large as *annulipes* and to exhibit differences in wing venation. The details given in the original description and key need some amplification before the species can be properly recognized. Mamaev (*in litt.*, 1975) says that he could not see any differences in the genitalia and that the main differences were in the larvae.

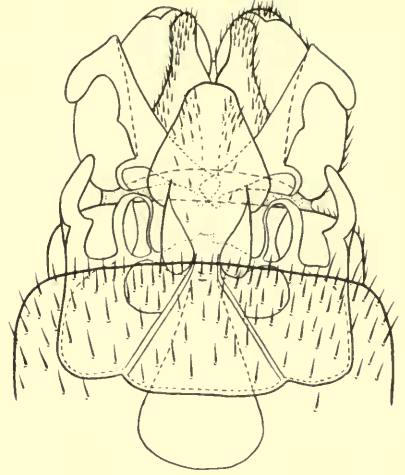
DISTRIBUTION. U.S.S.R. (Tula Region).



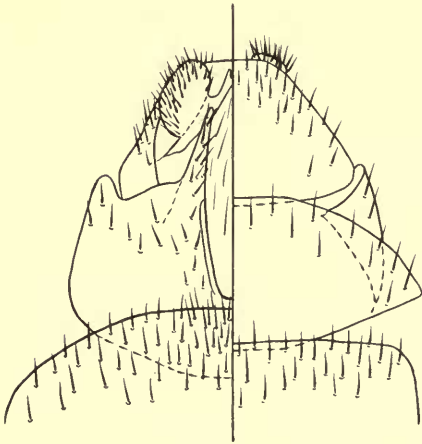
FIGS 4-8. *Exiliscelis californiensis*. 4, ♂ genitalia, dorsal (left) and ventral (right) views; 5, ♂ genitalia, posterior view; 6, ♂ genitalia, lateral view showing sperm pump; 7, ♂ sperm pump, dorsal (left) and ventral (right) views; 8, ♀ ovipositor, ventral (left) and dorsal (right) views.



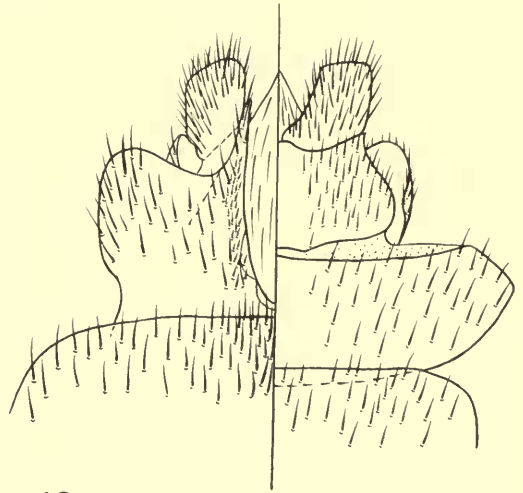
9



10



11



12

FIGS 9-12. *Synneuron* species. 9, *annulipes*, ♂ genitalia, ventral view; 10, *decipiens*, ♂ genitalia, ventral view; 11, *annulipes*, ♀ ovipositor, ventral (left) and dorsal (right) views; 12, *decipiens*, ♀ ovipositor, ventral (left) and dorsal (right) views.

***EXILISCELIS* gen. n.**

(Text-figs 1, 3-8)

Type-species: *Exiliscelis californiensis* sp. n.

Small black Scatopsid-like flies with long shining wings. Rather ant-like in general appearance. Similar to *Synneuron*, but readily distinguishable by the characters in the above key (Text-fig. 1).

DIAGNOSIS. Head longer than broad. Eyes separated by one facet width above antennae, approaching each other, but well separated below antennae. Three ocelli. Antennae 16-segmented, all segments closely applied to each other, without necks, and covered with dense short setae. Palpi 4-segmented, basal two segments short and squat, segment three enlarged and bearing a large sensory pit, segment four long and narrow.

Thorax somewhat compressed laterally. Pronotum reduced but forming a complete collar. Propleuron small. Anterior spiracle in front of anepisternite. Sternopleuron well developed. Meron much reduced so that mid and hind coxae almost touch. All coxae strongly developed. Mid and hind coxae directed posteriorly. Femora long and slender; tibiae long, straight and slender. Fore tibiae with a single small but distinct spur; mid and hind tibiae with two short spurs. Pulvilli absent. Empodium reduced to a small scale with marginal hairs. Tarsal claws with a single prominent basal tooth.

Wing (Text-fig. 3) long and narrow with only a very slight anal lobe and no alula. R_4 present, short and ending in costa shortly after apex of R_1 . R_s and M fused for a distance of about half the basal section of R_s . Median fork complete. Basal section of M_{3+4} long and in line with a very short $m-cu$. Anal vein absent or represented by a short, weak, basal spur.

Abdomen with seven unmodified pregenital segments. Abdomen somewhat flattened dorso-ventrally and widened toward posterior. ♂ genitalia (Text-figs 4-7) with sperm-pump closely associated with hypopygium and connecting with the exterior via a heavily sclerotized trifid penis-sheath. ♀ genitalia (Text-fig. 8) with 2-segmented ovipositor and two heavily sclerotized spermathecae anterior to a pair of small sclerotized 'accessory glands'.

DISTRIBUTION. Nearctic

Exiliscelis californiensis sp. n.

(Text-figs 1, 3-8)

DIAGNOSIS. Head about 0.6 mm long, shining black with short sparse hairs. Eyes extending ventrally to the mouth margin, covered with a short pubescence. Ocelli set on slightly raised tubercles, equally spaced, median one about half the size of the laterals. Scape and pedicel about equal in size. Flagellar segment 1 slightly longer than wide, 2-13 distinctly wider than long, 14 about twice as long as wide. Proboscis and palpi beset with hairs of various lengths.

Dorsum of thorax shining black except for slight orange coloration on the humeri of the male; evenly covered with short setae that become longer above the wings, but without distinct supra-alar setae. Pleurae and postnotum somewhat reddish black. Anepisternum strongly developed, but with only a few weak hairs. Sternopleura with weak sparse hairs ventrally. Pleurotergite well developed. Scutellum not very prominent and sparsely covered with weak setae, which are quite long toward the posterior margin. Postnotum about 1.5 times the length of the scutellum, bare of setae. Capitulum of haltere twice as long as pedicel, both without distinct setae, except for about three very short setae at the base of the capitulum.

Mid coxa slightly shorter than hind coxa which is shorter than fore coxa. Tibiae widening slightly and evenly toward the apex, with a comb of pale setae on the posterior side at their apex. Tarsi slender and unmodified, hind basitarsus about twice as long as second tarsal segment.

Wing (Text-fig. 3) 3.0-3.5 mm long, evenly covered on both sides with microtrichia. Basal section of vein M_{3+4} bare, all other veins bearing macrotrichia (only 2 or 3 on petiole of median fork). Veins posterior to R_s well developed, but not heavily pigmented. Sc very short and ending free, but continued as a fold to beyond the fork of the radius. R_5 about six times length of R_4 . Costa ending nearly half way between ends of veins R_5 and M_1 . Petiole of median fork (M_{1+2}) about equal to basal section of R_s . Vein $m-cu$ in line with basal section of M_{3+4} and these two veins combined are about equal to the basal section of R_s . A distinct

fold running from near wing base through the centre of the basal section of M_{3+4} and continuing into cell M_2 . Cu_2 faintly represented, running parallel with Cu to just after the junction with $m-cu$. Marginal hairs around wing are dense from the end of the costa to the remnant anal lobe, very sparse from here to wing base.

Abdomen shining black. Genitalia as described for genus and illustrated in Text-figs 4-7 (♂) and Text-fig. 8 (♀).

MATERIAL EXAMINED.

Holotype ♂ (dry-pinned), U.S.A.: California, Amador Co., Pioneer, 8.v.1961 (*O. W. Richards*) (BMNH).

Paratypes. U.S.A.: same data as holotype, 1 ♂, 1 ♀ (slide mounted).

A further single female is very much larger than the type-series (wing-length 6.0 mm). This specimen also has unequal hind tibial spurs and a much longer head and so may be a second species. Its data are: U.S.A.: Oregon, Humbug Mts, Curry Co., 20.vi.1939 (*T. Aitken*) (B. Brookman coll., in USNM, Washington (per E. F. Cook)).

CANTHYLOSCELIDAE Rodendorf

Corynoscelinae Enderlein, 1912 : 264. Type-genus: *Corynoscelis* Boheman, 1858 [junior homonym of *Corynoscelis* Burmeister, 1847].

Corynoscelidae Enderlein; Enderlein, 1936 : 56.

Canthyloscelididae Rodendorf, 1951 : 64. Type-genus: *Canthyloscelis* Edwards, 1922.

Corynoscelinae [Enderlein]; Tollet, 1959 : 144. [Proposed as new subfamily.]

Hyperoscelidae Hardy & Nagatomi, 1960 : 263. Type-genus: *Hyperoscelis* Hardy & Nagatomi [replacement name for *Corynoscelis* Boheman]. **Syn. n.**

Hyperoscelididae Hardy & Nagatomi; Rodendorf, 1964 : 16.

NOMENCLATURE. The *International Code of Zoological Nomenclature* (1964), Article 23d(i), states that the oldest valid family-group name must be used. The homonymy of *Corynoscelis* Boheman makes the family name based on it invalid (Article 39). If the two families considered in this paper are regarded as one composite family, the valid family-group name would be Synneuridae Enderlein, 1936, as this name has priority. Where they are regarded as two separate families, as in the present work, the name Canthyloscelidae, proposed as Canthyloscelididae by Rodendorf (1951), predates Hyperoscelidae Hardy & Nagatomi (1960), and so is the valid name for the restricted family including *Hyperoscelis* and *Canthyloscelis*. Thus the family name Hyperoscelidae must be changed: for Canthyloscelidae if the family is restricted to *Canthyloscelis* and *Hyperoscelis*, or Synneuridae if *Synneuron* and *Exiliscelis* are included.

I regard it as both unnecessary and undesirable to change the family-group name yet again for a group that, though small, has already been widely discussed outside the realm of basic taxonomy: in fields such as the evolution of Diptera (Rodendorf, 1964; Mamaev, 1968), zoogeography (Hennig, 1960; 1965), anatomy, ecology, physiology and development (Rodendorf, 1951; Hennig, 1954; Krivosheina & Mamaev, 1967; Mamaev & Semenova, 1969; Krivosheina, 1969), as well as important general faunal lists (e.g. Cook, 1965; 1967; Martinovsky, 1972) and key

works (e.g. Seguy, 1951; Brues, Melander & Carpenter, 1954; Bei-Bienko, 1969; Colless & McAlpine, 1970; Hennig, 1973). It is to be hoped that this latest change 'in the interests of stability' is the last of such changes.

DIAGNOSIS. As in key to families (p. 70).

DISTRIBUTION. South America, New Zealand and Palaearctic.

KEY TO THE GENERA

- 1 Median fork complete. Claws simple. Antennae only about two-thirds length of thorax. (Palaearctic) **HYPEROSCELIS** (p. 78)
 - Median fork with M_2 interrupted at base. Claws with a comb-like or toothed basal enlargement. Antennae as long as head and thorax together. (Neotropical and New Zealand). **CANTHYLOSCELIS** (p. 83)

HYPEROSCELIS Hardy & Nagatomi

(Text-figs 13-19)

Corynoscelis Boheman, 1858 : 56. Type-species: *Corynoscelis eximia* Boheman, 1858, by monotypy. [Preoccupied by *Corynoscelis* Burmeister, 1847.]

Spiloptera Zetterstedt, 1860 : 6487. Type-species: *Spiloptera arctica* Zetterstedt, 1860, by monotypy. [Proposed in synonymy in footnote.]

? *Eucorynoscelis* Rodendorf, 1951 : 65. Type-species: *Corynoscelis eximia* Boheman, 1858, by monotypy.

Hyperoscelis Hardy & Nagatomi, 1960 : 264. [Replacement name for *Corynoscelis* Boheman.]

NOMENCLATURE. Zetterstedt's footnote (1860) stating that he had prepared a description of *Corynoscelis* under the name *Spiloptera* produces a problem of nomenclature. Jerdon (1862) applied the name *Spiloptera* to a genus of birds and Oates (1889), considering *Spiloptera* Jerdon a junior homonym of *Spiloptera* Zetterstedt, proposed the name *Elachura* as a replacement name. *Elachura* is currently regarded as a junior synonym of *Spelaeornis* David & Oustalet, 1877 (Peters, 1964). Hardy & Nagatomi (1960), realising the homonymy of *Corynoscelis* Boheman and *Corynoscelis* Burmeister, proposed the replacement name *Hyperoscelis* for Boheman's genus. At that time their action was perfectly correct, but since then the *International Code of Zoological Nomenclature* (ICZN, 1964) has been altered so that Article 11d now states that a name proposed in synonymy is to be regarded as available if it has been used as a primary homonym. Such is the case with *Spiloptera* Zetterstedt, which is therefore the oldest available name for this genus. However, since *Spiloptera* Zetterstedt has never been referred to in entomological literature since 1860, I am regarding it as a *nomen oblitum* and intend to apply to the International Commission on Zoological Nomenclature to ratify this.

The name *Eucorynoscelis* also predates *Hyperoscelis*, but I am not certain of its validity. It appears in the legend of a figure in Rodendorf (1951) in the combination *Eucorynoscelis eximia* Boheman. It is not mentioned in the text.

I have not found the name anywhere else. If this is its only mention then it is an obvious synonym of *Corynoscelis* and *Hyperoscelis* (same type-species by monotypy), but since it may be described elsewhere (it is included in his family Canthyloscelidae), I have applied it to this genus with reservations.

DIAGNOSIS. Three ocelli present, median one reduced. Antennae 16-segmented, loosely jointed. Eyes narrowly separated above and below antennae. Gena small, mouth margin very close to bottom of eyes. First segment of palpi very small, second rounded, third and fourth elongate. Minute single spurs on fore and mid tibiae. Tarsal claws simple. Empodium broadly rounded and fringed with hairs. Hind femur swollen. Hind tibia slender and curved to fit femur. Fore and mid legs yellow, hind legs variegated. Wings with posterior veins well pigmented. A short vein R_4 present and usually ending in costa, otherwise incomplete and ending free. Vein $r-m$ represented by a long fusion. Median fork complete. Cu_2 very weakly present. Anal vein reaching margin, but weak towards wing base. Basal abscissa of M_{3+4} in line with short $m-cu$. Seven unmodified pregenital segments. ♂ with tergite 8 almost atrophied. ♀ with 2-segmented ovipositor and one simple spermatheca.

DISTRIBUTION. Palaearctic.

DISCUSSION. Boheman (1858) first described *Corynoscelis eximia* from material sent by Holmgren from Swedish Lapland. In the same year Loew (1858) described and figured the same specimen(s). Presumably because he knew that Boheman was describing it, Loew did not give it a name. Zetterstedt (1860) described it using Boheman's name, but in a footnote stated that he too had already seen Holmgren's specimen and had prepared his description of it under the name *Spiloptera arctica*. Mik (1886), still discussing the same material, though probably not from first hand experience, noted its superficial similarity to certain Empidid genera (*Oedalea* and *Hybos*) and confirmed this similarity to the latter genus when he (Mik, 1900) obtained a specimen from Rumania which he considered to be the same species (but see p. 83). Lundström (1910) described what he thought was the female of *eximia*, but the sex and identity of these specimens are in doubt (see p. 82).

Dahl (1911) described a larviform female insect as the female of *Corynoscelis*. The specimen had been found on an empty lepidopterous pupa and, assuming it to be parasitic, Dahl discussed its relationship with fleas, etc., as well as Scatopsidae and Phoridae. Bergroth (1912) was quick to point out Lundström's (1910) description attributed to the female of *eximia* as a normally full-winged fly, but agreed with Dahl that his specimen belonged near *Corynoscelis* and *Scatopse* in the Bibionidae. Enderlein (1912), without seeing the specimen himself, considered Dahl's specimen as more Mycetophilid-like and erected a new genus and species for it, *Dahlia larviformis*. In 1936 Enderlein put it in a separate subfamily of Mycetophilidae. There it remained until Bartošová & Dušková (1958) described a second species, *Dahlia hirta*, from Czechoslovakia. Their good description and figures enabled Stýs (1960) to re-examine the affinities of *Dahlia* and he realized that both species were moths and probably Psychidae. *Dahlia larviformis* Enderlein is now regarded as a synonym of *Solenobia triquetrella* (Hübner, 1812) (Lepidoptera: Psychidae) (vide Dierl, 1968).

Meanwhile, Frey (1916) had recorded another specimen from Finland, after

which no further specimens of the genus are known to me until Hardy & Nagatomi (1960) described a second species, *insignis*, from a single male from Japan. Mamaev & Krivosheina (1969) reared large numbers of *Hyperoscelis* of two species from larvae found in rotting wood. By examining type-material of *eximia* they were correctly able to decide which species was undescribed. The undescribed species, *veternosa*, was described from 21 males and the sexes of the material of *eximia* were not noted, so it was not until Martinovsky (1972) that a true female *Hyperoscelis* was adequately described. This is the most recent published record of *Hyperoscelis* known to me.

Of the three described species I can only recognise two as valid, and these are separable by the following key.

KEY TO SPECIES OF *Hyperoscelis*

- 1 Length of R_5 equal to distance between the base of M_{1+2} and the fork of R_{4+5} . Basal part of M not parallel with R_1 , unsclerotized, without macrotrichia; macrotrichia absent between these two veins. Tergite 8 of male with lateral processes and a deep median emargination, claspers as Text-fig. 17, sternite 9 with marked lateral extensions (Text-figs 13, 15-17).
 Female ovipositor as Text-fig. 19 *eximia* Boheman (p. 80)
- R_5 shorter than distance between base of M_{1+2} and the fork of R_{4+5} . Basal part of M before the $r-m$ fusion parallel with R_1 , heavily sclerotized and covered with macrotrichia; macrotrichia present on wing membrane between these two veins. Tergite 8 of male smoothly rounded with a shallow median emargination, claspers as Text-fig. 18, sternite 9 without marked lateral extensions (Text-fig. 14).
veternosa Mamaev & Krivosheina (p. 83)

Hyperoscelis eximia (Boheman)

(Text-figs 13, 15-17, 19)

Corynoscelis eximia Boheman, 1858 : 56. Syntypes 2 ♂, 1 ♀, SWEDEN: Tarna [65°43' N, 15°17' E], Laxfjellet, 15-18.vii. (*A. E. Holmgren*) (NR, Stockholm) [examined].

Hyperoscelis insignis Hardy & Nagatomi, 1960 : 265. Holotype ♂, JAPAN: Hataganaru (Tazima), 26.v.1955 (*E. Fujita*) (KUF, Fukuoka) [examined]. **Syn. n.**

DIAGNOSIS. As in key to species. Some authors (Hardy & Nagatomi, 1960 and Martinovsky, 1972) have overlooked the small first palpal segment and considered the palps 3-segmented. All specimens I have seen have 4-segmented palps.

MATERIAL EXAMINED.

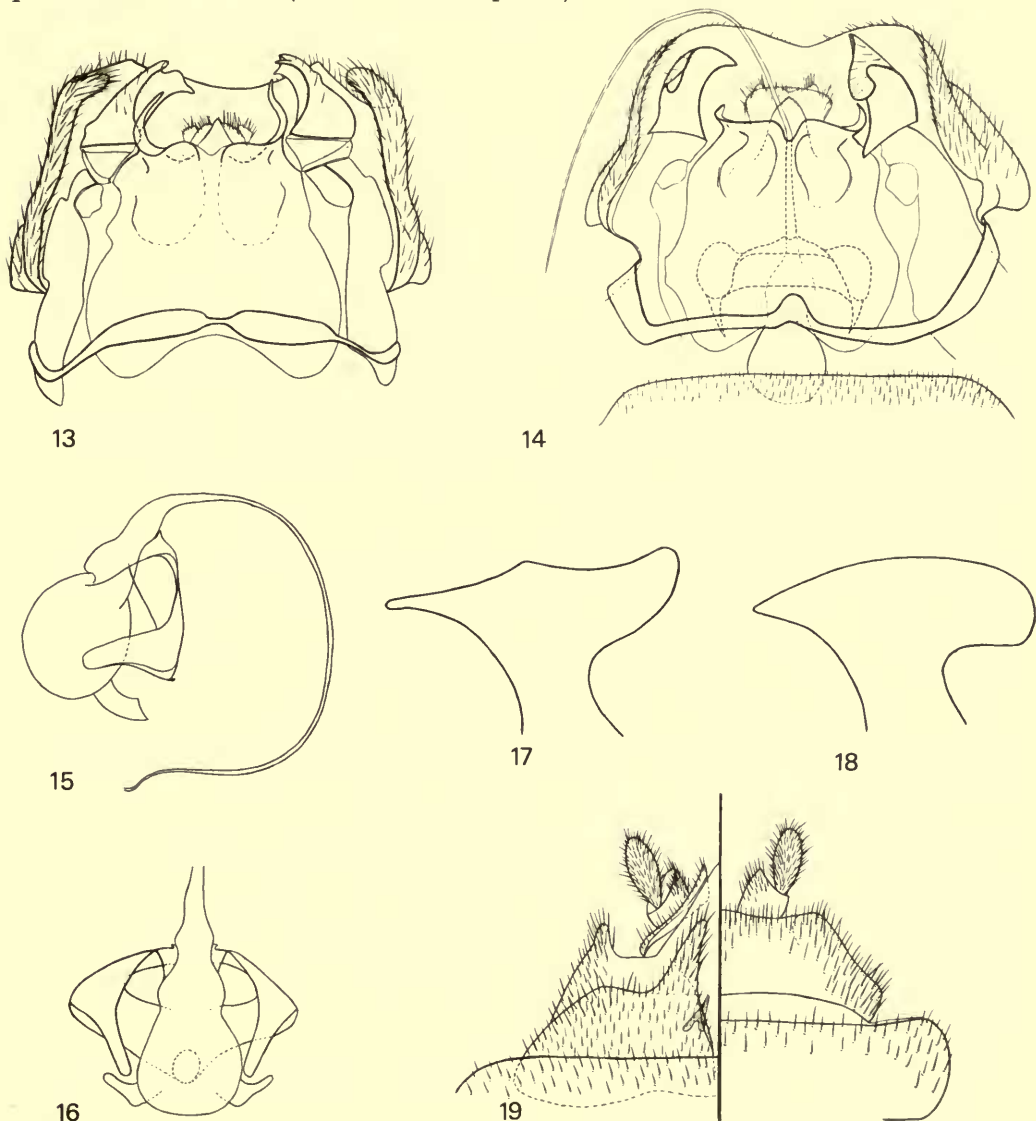
2 ♂, 1 ♀ syntypes of *eximia*, SWEDEN (details in synonymy). Holotype ♂ of *insignis*, JAPAN (details in synonymy).

CZECHOSLOVAKIA: Moravia, Bedrichov bei Rymarov (Bezirk Sumperk), 500 m, 18.vi.1970 (*J. Martinovsky*), 1 ♀ (coll. J. Martinovsky, Olomouc); Moravia, Josefova u Branne, 20.vi.1972 (*J. Martinovsky*), 1 ♀ (BMNH).

DISCUSSION. Boheman's specimens are in good condition. No holotype was originally recorded and no lectotype has been designated since. As there is no

suggestion that the series consists of more than one species, I have not selected a lectotype. The genitalia of one of the males have been cleared and are in a microvial on the pin, and are figured here (Text-figs 13, 15-17).

Mik (1900) recorded a specimen of this species from Rumania, but his specimen proves to be *veternosa* (see under that species).



FIGS 13-19. *Hyperoscelis* species. 13, *eximia*, ♂ genitalia, ventral view; 14, *veternosa*, ♂ genitalia, ventral view; 15-17, *eximia* showing (15), ♂ sperm pump, lateral view, (16) ♂ sperm pump, ventral view, (17) outline of lateral view of ♂ clasper; 18, *veternosa*, outline of lateral view of ♂ clasper; 19, *eximia*, ♀ ovipositor, ventral (left) and dorsal (right) views.

Lundström (1910) and Frey (1916) recorded three specimens (as ♀) from three localities in Finland. Two of these specimens have been attacked by pest beetle and all that remains are three wing fragments and one antenna. One of the wing fragments shows the base of a strong vein R_4 which, estimated from the position of the medial veins, may be in the relative position of *eximia* rather than *veternosa*. Lundström's two specimens were from Ruovesi [61°59'N, 24°05'E] and Tuovilanlaks [c.63°N, c.28°E]. There is a bare celluloid strip on the pin of the Ruovesi specimen; whatever was mounted on it is lost except for a small piece of tissue which could be eggs. If it is eggs then the specimen must have been female, otherwise there is no way of sexing the original specimen. A separate mount of one antenna is part of this specimen. The Tuovilanlaks specimen is the specimen that Hardy & Nagatomi (1960) used to compare with their specimen from Japan and is a male of *veternosa*, misleading them into describing their specimen as a new species. Of Frey's specimen from Kangasala [61°30'N, 24°00'E] there is no trace on the pin. One, or two, of the wing fragments mentioned above belong to this specimen, but it remains unidentifiable. The Tuovilanlaks specimen and the remains of the other two specimens are in the University Museum, Helsinki, Finland.

Rodendorf (1951), in his discussion on the locomotory organs of Diptera, figures the wing of what he calls *Eucorynoscelis eximia* Boheman from Denmark. The status of the name *Eucorynoscelis* has already been discussed and I know of no specimen of this family from Denmark.

Hardy & Nagatomi (1960) described *H. insignis* from a single ♂. In structural details it does not differ from *eximia*, although there are quite distinct differences in the colour of the thorax and abdomen. In all other specimens of the genus examined in the present study the only yellow visible on these parts was around the anterior spiracle, otherwise the thorax and abdomen are dark reddish brown to black. In the Japanese specimen, most of the pronotum, the area of the anterior spiracle and the scutellum, particularly medially, are all yellow and the dorsum is yellow with three black stripes. The abdomen has yellow spots along the mid-dorsal line and the sternites are completely yellow. Despite these colour differences I have no hesitation in synonymizing *insignis* with *eximia*.

Mamaev & Krivosheina (1969) recorded *eximia* from the Maritime Province on the east coast of the U.S.S.R. Their specimens were bred from various types of rotting forest timber, mainly elm. Other series of larvae that were probably of this species were found in spruce wood much damaged by brown rot. These were from the Moscow and Yaroslavl Regions of the U.S.S.R. This material is in the IAEME, Moscow.

Martinovsky (1972) was the first to adequately describe and figure the female from his first specimen, which was found in a stand of *Rubus idaeus* L. in a mixed wood. His first specimen is in his private collection and he has kindly donated a second specimen to the BMNH.

DISTRIBUTION. Sweden, Czechoslovakia, U.S.S.R. (Maritime Province), Japan. Also probably in Finland and the Yaroslavl and Moscow Regions of U.S.S.R.

Hyperoscelis veteriosa Mamaev & Krivosheina

(Text-figs 14, 19)

Hyperoscelis veteriosa Mamaev & Krivosheina, 1969 : 936. Holotype ♂, U.S.S.R.: Ukraine, Rakhov, 17.vi.1966 (B. Mamaev) (IAEME, Moscow) [not examined].

DIAGNOSIS. As in key to species.

MATERIAL EXAMINED.

U.S.S.R.: same data as holotype, 2 ♂ (paratypes) (BMNH). RUMANIA: Bucharest, 1898 (*J. Mik*), 1 ♂ (NM, Vienna). FINLAND: Tuovilanlaks, 2.vi.1865, 1 ♂ (ZMU, Helsinki).

DISCUSSION. The type-material of 21 males was reared from larvae in spruce wood affected by brown rot.

In recording his specimen from Rumania, Mik (1900) noted that vein R_4 (by current terminology) is rudimentary and does not reach the costa. As this is a feature of *veteriosa*, the specimen was re-examined and found to be ♂ *veteriosa*.

While the identity of Lundström's Ruovesi specimen and Frey's Kangasala specimen remains in doubt as the specimens are destroyed (see above under *eximia*), Lundström's other specimen, from Tuovilanlaks, was described and figured by Hardy & Nagatomi (1960) as *eximia*. The specimen is mounted on a slide and is a ♂ *veteriosa*.

DISTRIBUTION. Finland, Rumania, U.S.S.R. (Ukraine: Transcarpathian Mts).

CANTHYLOSCELIS Edwards

(Text-figs 20-25)

Canthyloscelis Edwards, 1922 : 268. Type-species: *Canthyloscelis antennata* Edwards, 1922, by original designation.

DIAGNOSIS. Two large lateral ocelli, small median ocellus present (subgenus *Araucoscelis*) or absent (subgenus *Canthyloscelis*). Antennae 16-segmented, simple to distinctly pectinate, at least as long as head and thorax combined. Palpi 4-segmented, long and slender. Tibial comb well developed (*Araucoscelis*) or poorly developed (*Canthyloscelis*). Tarsal claws with a large basal lobe bearing a number of small teeth. Empodium large and fleshy. Hind femur greatly swollen, often with a row of small pegs on the ventral surface. Hind tibia slender and curved to fit tightly against femur. Wings with posterior veins almost as heavily pigmented as anterior veins. A short R_4 present and ending in costa. $r-m$ represented by a long fusion. M_2 interrupted at base. Males with only 2 or 4 (*Canthyloscelis*) or 6 (*Araucoscelis*) unmodified pregenital segments. Ovipositor 2-segmented. One spermatheca, strikingly modified in *Canthyloscelis* (Text-fig. 25) or simple in *Araucoscelis*.

DISCUSSION. Edwards (1922) described *Canthyloscelis* for three species in New Zealand. In 1930, he described a second subgenus (*Araucoscelis*) for two species from South America, to which he later (1934) added a third species, also from South America. In describing a fourth South American species, Tollet (1959) separated the South American species into two subgenera on the basis of the pectinate

antennae of the male of one species. A fourth New Zealand species is described here.

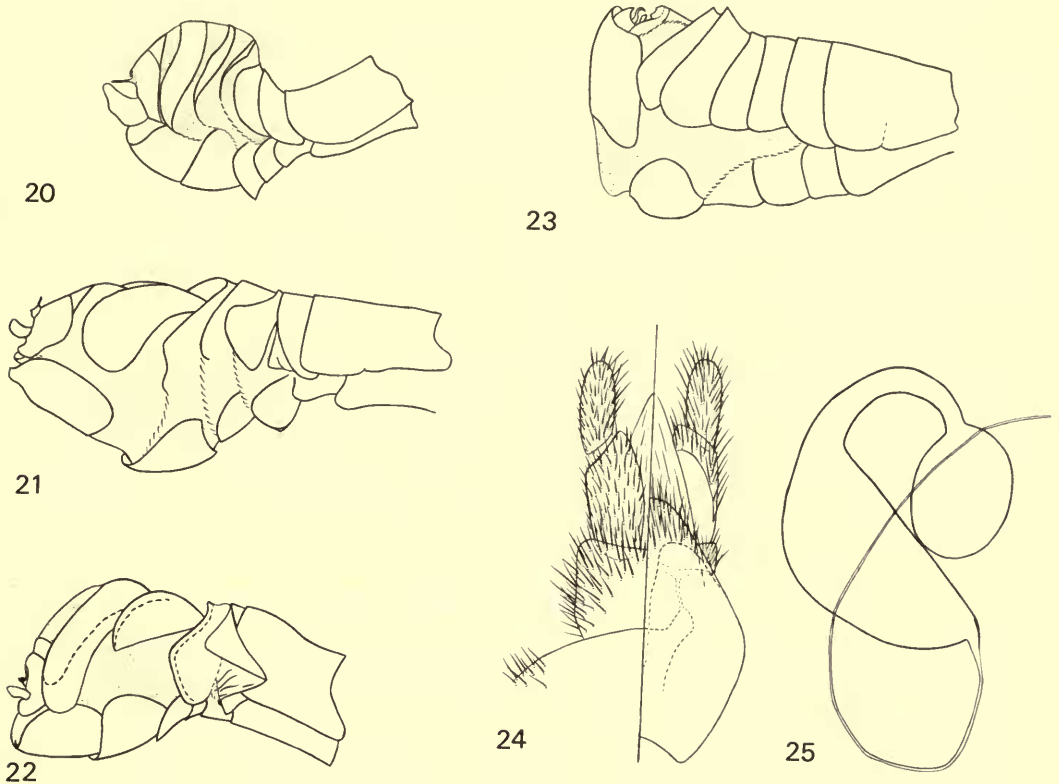
The sharp distinctions between the New Zealand and South American species-groups are clear; these could well be regarded as separate genera, but it is convenient to leave them as congeners for the time being, thereby expressing the opinion that they are sister-groups and that together they are the sister-group of *Hyperoscelis* (as proposed by Hennig, 1960). I would also agree with Hennig (op. cit.) that the South American species do not merit separation into two subgenera purely on the basis of whether or not the male antennae are pectinate, a patently derived character. Certainly the South American species do not differ in any fundamental character, and with the species synonymy given here such a division serves no useful purpose.

DISTRIBUTION. New Zealand and South America.

KEY TO SUBGENERA AND SPECIES OF *Canthyloscelis*

- 1 Median ocellus absent. Eyes narrowly separated above antennae. Flagellar segments with distinct necks. Gena well developed, so lower margin of eyes well separated from mouth margin. Meron well developed. Hind femur swollen in apical two-thirds. Wing vein R_5 not thickened towards tip. Basal abscissa of vein M_{3+4} almost vertical, joining *Cu* before the posterior fork. Two or 4 unmodified pregenital segments in male. Female with single complex spermatheca. (New Zealand). (Subgenus **CANTHYLOSCELIS**) 2
- Small median ocellus present. Eyes broadly in contact above antennae. Mouth margin very close to bottom of eyes. Meron somewhat reduced. Hind femur swollen from near base. Wing vein R_5 thickened beyond fork with R_4 . Basal abscissa of M_{3+4} almost vertical and in line with short *m-cu*. Six unmodified pregenital segments in male. Female with single simple spermatheca. (South America). (Subgenus **ARAUCOSCELIS**) 5
- 2 Wings with dark mark near apex. Pleurae at least somewhat darkened. Eyes of ♂ almost touching above antennae. ♂ abdomen with only two unmodified pregenital segments. 3
- Wings completely clear. Pleurae uniformly yellowish. ♂ eyes distinctly separated above antennae. ♂ abdomen with four unmodified pregenital segments.
Microtrichia extensive on upper as well as lower surface of wing, covering entire wing except for extreme base. **claripennis** (p. 89)
- 3 All coxae pale yellowish. Hind basitarsus about twice as long as second tarsal segment. 4
- Hind coxae shining black. Hind basitarsus about same length as second tarsal segment.
Thorax uniformly reddish. Wing lacking microtrichia on costal, R_1 , basal cells and basal areas of cells R_5 and M_2 , and restricted to outer parts in cells R_4 , M_{3+4} , *Cu* and anal. Tergite 9 of male simple **nigricoxa** (p. 88)
- 4 Thorax with pale ground colour and three more or less distinct stripes. Wing lacking microtrichia on costal, R_1 , basal, most of anal cells and extreme bases of other cells. Tergite 9 of male with a pair of long fine points. **antennata** (p. 87)
- Thorax unstriped. Microtrichia widely distributed on both wing surfaces, absent from most of costal, *Cu*, anal and basal cells and extreme bases of cells R_1 and M_2 . Tergite 9 of male emarginated. **balaena** (p. 88)

- 5 Wings unmarked or with only very vague marking at wing tip. Palpi pale. Antennae of ♂ strongly pectinate *pectinata* (p. 86)
 - Wings with distinct marking toward tip and also frequently in costal cell and on hind margin. Palpi dark. Antennae of ♂ at most slightly serrate *pictipennis* (p. 86)



FIGS 20-25. *Canthyloscelis* species. 20, *antennata*, ♂ abdomen, lateral view; 21, *nigricoxa* ♂ abdomen, lateral view; 22, *balaena*, ♂ abdomen, lateral view; 23, *claripennis*, ♂ abdomen, lateral view; 24, 25, *antennata* ♀ showing (24) ovipositor, ventral (left) and dorsal (right) views, (25) spermatheca.

Subgenus *ARAUCOSCELIS* Edwards

Araucoscelis Edwards, 1930 : 90 [as subgenus of *Canthyloscelis* Edwards]. Type-species: *Canthyloscelis pectinata* Edwards, 1930, by original designation.

Chiliscelis Tolle, 1959 : 146 [as subgenus of *Canthyloscelis* Edwards]. Type-species: *Canthyloscelis pictipennis* Edwards, 1930, by original designation.

DIAGNOSIS. As in key on p. 84.

DISCUSSION. Hennig (1960) suggested the above synonymy. Cook (1967), in error, has stated *valdiviana* to be the type-species of *Chiliscelis*.

DISTRIBUTION. South America.

Canthyloscelis (Araucoscelis) pectinata Edwards

Canthyloscelis (Araucoscelis) pectinata Edwards, 1930 : 90. Holotype ♂, ARGENTINA: Terr. Rio Negro, Puerto Blest, L. Nahuel Huapi, 2-3.xii.1926 (*F. & M. Edwards*) (BMNH) [examined].

DIAGNOSIS. Antennae of male with first nine flagellar segments bearing a long ventral basal branch and a slight node at the apex. Flagellar segments with distinct necks. Palpi dark. First hind tarsal segment about twice as long as second. Wings clear or with a very vague subapical cloud, posterior veins rather pale. Head, thorax and abdomen reddish brown with three indistinct thoracic stripes. All coxae and fore and mid legs pale yellow, getting darker towards terminal tarsal segments (femur sometimes darkened above). Hind legs with reddish brown band on apical half and at apex of femur, tibiae and tarsi darkened. Male with sternite 7 greatly enlarged, bowl-shaped, with genitalia directed dorsally. Tergite 9 with a pair of narrow outwardly curved processes. Claspers relatively small and broad, with a longitudinal crest, so that it is T-shaped in cross-section. Another pair of long curved finely pointed processes below this (? dististyle).

MATERIAL EXAMINED.

Holotype ♂, ARGENTINA (details in synonymy).

ARGENTINA: same data as holotype, 10 ♂, 3 ♀; Terr. Rio Negro, L. Correntoso, 18-25.xi.1926 (*F. & M. Edwards*), 3 ♂. CHILE: S., Llanquihue prov., Casa Pangué, 4-10.xii.1926 (*F. & M. Edwards*), 1 ♀. (All paratypes; all in BMNH.)

DISTRIBUTION. Border area of Argentina and S. Chile, near L. Nahuel Huapi.

Canthyloscelis (Araucoscelis) pictipennis Edwards

Canthyloscelis (Araucoscelis) pictipennis Edwards, 1930 : 92. Holotype ♀, ARGENTINA: Terr. Rio Negro, Lake Frias, 3.xii.1926 (*F. & M. Edwards*) (BMNH) [examined].

Canthyloscelis apicata Edwards, 1934 : 186. 4 syntypes ♂, CHILE: Comudes, 16-17.ii.1902 (*S. Schonemann*) (1 in BMNH) [examined]. **Syn. n.**

Canthyloscelis (Chiliscelis) valdiviana Tollet, 1959 : 147. Holotype ♂, CHILE: Valdivia prov., nr L. Panguipulli, Shoshnenco, 200 m, 4-6.iii.1955 (*L. E. Peña*) (IRSNB, Brussels) [examined]. **Syn. n.**

DIAGNOSIS. Flagellar segments of male slightly serrate, loosely jointed but without obvious necks. Palps pale yellow. First hind tarsal segment about 1.5 times as long as second. Wings with dark subapical band and slightly darkened costal cell. Posterior veins darkened, as usual. Head (usually), thorax and abdomen dark reddish brown, thorax unstriped. Legs as *pectinata*, except that hind coxae dark in the Casa Pangué ♂. Sternite 7 of male greatly enlarged, bowl-shaped with genitalia directed dorsally. Tergite 9 with pair of broad, straight median processes. Claspers broad, triangular, with small inner lateral processes. The processes below this (? dististyles) short, straight and blunt, slightly bulbous-tipped.

MATERIAL EXAMINED.

Holotype ♀ of *pictipennis*, ARGENTINA: (details in synonymy). 1 ♂ syntype of *apicata*, CHILE (details in synonymy). Holotype ♂ of *valdiviana*, CHILE (details in synonymy).

CHILE: Llanquihue, Casa Pangué, xii. 1926 (*R. & E. Shannon*), 1 ♂ (USNM, Washington); Chiloe Island, Dalcahue, 10-12.ii.1957 (*L. E. Peña*), 1 ♀ (allotype of *valdiviana*) (IRSNB, Brussels).

DISCUSSION. Edwards (1934) recorded a specimen as the male of *pictipennis*, which he had described from a single female. I have examined this specimen and find it the same species as the single male syntype of *apicata* that is in the BMNH. *C. apicata* was described from four male syntypes, the other three are stated to be in the Zoological Museum of Berlin (now the Zoologisches Museum für Naturkunde der Humboldt-Universität) and have not been examined in the present study.

C. valdiviana was described from several males and two females, and the male holotype and female allotype were examined in the present study. I can see no difference at the species level between the holotype of *valdiviana* and the BMNH type of *apicata* and so am confident in synonymising these two species. Thus *apicata*, the male attributed to *pictipennis* by Edwards (1934), and *valdiviana* are all the same species.

The two females I have seen are the type of *pictipennis* and the allotype of *valdiviana*. Slight differences in the structure of the ovipositor are detectable, but are not enough to regard the two as distinct species and colour differences are no more than the variety shown by the males. The locality of the type of *pictipennis*, although actually in Argentina, is closer to the locality of the males described as *valdiviana* and *pictipennis*, than are the females described as *valdiviana*. I therefore regard all these as a single species, i.e. *apicata* and *valdiviana* are synonyms of *pictipennis*.

DISTRIBUTION. Chile and the border of Argentina between 37° and 43°S (I have not been able to trace Comudes, the type-locality of *apicata*).

Subgenus *CANTHYLOSCELIS* Edwards

Canthyloscelis Edwards, 1922 : 268.

DIAGNOSIS. As in key on p. 84.

DISCUSSION. Four species are recognized in this subgenus. They could be separated into two species-groups, namely the *antennata*-group (*antennata*, *nigricoxa*, *balaena*) and the *clariipennis*-group (*clariipennis*), on the characters in the first half of couplet 2 of the key on p. 84.

DISTRIBUTION. New Zealand.

Canthyloscelis (Canthyloscelis) antennata Edwards

(Text-figs 20, 24-25)

Canthyloscelis antennata Edwards, 1922 : 268. Holotype ♂, NEW ZEALAND: Wainuiomata, in forest, 14.xii.1920 (*G. V. Hudson*) (BMNH) [examined].

DIAGNOSIS. Eyes of male almost touching above antennae. Dorsum of thorax with pale ground colour and three more or less distinct stripes. Pleura somewhat darkened. Wings with dark subapical band. Wings with microtrichia restricted to marginal areas on upper surface, lower surface lacking microtrichia in costal, R_1 , basal and most of anal cells and extreme bases of other cells. All coxae pale yellowish. Hind basitarsus about twice as long

as second tarsal segment. Male abdomen (Text-fig. 20) with two unmodified pregenital segments. Tergite nine of male with a pair of long fine points.

MATERIAL EXAMINED.

Holotype ♂, NEW ZEALAND (details in synonymy).

NEW ZEALAND: same data as holotype, 2 ♂ (paratypes); no locality (*G. V. Hudson*), 1 ♂, 1 ♀ (paratypes); Ohakune, 20.xi.1919 (*T. R. Harris*), 1 ♂; Ohakune, xi. 1922 (*T. R. Harris*), 1 ♂, 1 ♀; Ohakune, 1-9.iv.1923 (*T. R. Harris*), 1 ♂, 1 ♀; Ohakune, 2060', 1.iii.1919 (*T. R. Harris*), 2 ♀; Ohakune, 2060', 9.iv.1920 (*T. R. Harris*), 2 ♀; no locality, 1928 (*G. V. Hudson*), 3 ♂, 1 ♀. (All in BMNH.)

DISTRIBUTION. New Zealand.

Canthyloscelis (Canthyloscelis) nigricoxa Edwards

(Text-fig. 21)

Canthyloscelis nigricoxa Edwards, 1922 : 269. Holotype ♂, NEW ZEALAND (*G. V. Hudson*) [BMNH] [examined].

DIAGNOSIS. Eyes almost touching above antennae. Dorsum of thorax uniformly reddish. Pleurae somewhat darkened. Wings with dark subapical band. Wings with microtrichia restricted to marginal areas on upper surface and lower surface lacking microtrichia on costal, R_1 , basal cells and basal areas of cells R_5 and M_2 , and restricted to outer parts in cells R_4 , M_{3+4} , Cu and anal. Hind coxae shining black, others yellowish. Hind basitarsus about equal in length to second tarsal segment. Male abdomen (Text-fig. 21) with two unmodified pregenital segments. Tergite 9 of male simple.

MATERIAL EXAMINED.

Holotype ♂, NEW ZEALAND (details in synonymy).

DISTRIBUTION. New Zealand.

Canthyloscelis (Canthyloscelis) balaena sp. n.

(Text-fig. 22)

DIAGNOSIS. Eyes narrowly separated above antennae. Dorsum of thorax uniformly light brown. Pleurae similarly coloured, becoming darker towards ventral parts. Wings with dark subapical band. Wings with microtrichia widespread on dorsal and ventral surfaces. Wings lacking microtrichia in most of costal, Cu , anal and basal cells and extreme bases of cells R_1 and M_2 . R_1 ending beyond the level of the beginning of vein M_2 . All coxae pale yellowish. Hind basitarsus more than twice length of second tarsal segment.

Male abdomen (Text-fig. 22) with two unmodified pregenital segments (the second short and narrow). Tergite 3 folded, with the fold running across the abdomen, the lateral corners forming anteriorly directed processes, apical median area strongly emarginated. Tergite 4 weakly developed and medially emarginated. Tergite 5 so heavily emarginated that it appears as two lateral semicircular plates. Tergite 6 more distorted to appear as two crescent-shaped plates joined at their antero-dorsal ends. Tergites 7 and 8 simple. Tergite 9 with short broad points separated by a shallow evenly curved emargination. Claspers very small and rounded.

MATERIAL EXAMINED.

Holotype ♂, NEW ZEALAND: 1928 (*G. V. Hudson*), no. 136q (BMNH).

DISCUSSION. The specimen was in the series of *antennata*, but from the structure of the abdomen I would regard it as closer to *nigricoxa*. The structure of the abdomen and the extensive microtrichia of the wings readily distinguish this species from the others of the *antennata*-group.

DISTRIBUTION. New Zealand.

Canthyloscelis (Canthyloscelis) claripennis Edwards

(Text-fig. 23)

Canthyloscelis claripennis Edwards, 1922 : 268. Holotype ♂, NEW ZEALAND (*G. V. Hudson*) (BMNH) [examined].

DIAGNOSIS. Eyes of male distinctly separated above antennae. Dorsum of thorax with pale ground colour and three vague, dull brown, (almost) contiguous stripes. Pleurae uniformly yellowish. Wings completely clear. Wings with microtrichia extensive on upper as well as lower surface of wing, covering entire wing except for extreme base. All coxae pale yellowish. Hind basitarsus about twice as long as second tarsal segment. Male abdomen (Text-fig. 23) with four unmodified pregenital segments. Tergite 9 with a broad simple flange.

MATERIAL EXAMINED.

Holotype ♂, NEW ZEALAND (details in synonymy).

NEW ZEALAND: Ohakune, i. 1920 (*T. R. Harris*), 1 ♂; Ohakune, 15.xii.1922-15.i.1923 (*T. R. Harris*), 1 ♀; Ohakune, v. 1922 (*J. W. Campbell*), 1 ♀. (All in BMNH.)

DISCUSSION. The second ♂ is the specimen that Edwards (1930) mentions as a fourth New Zealand species of *Canthyloscelis*.

DISTRIBUTION. New Zealand.

CHECKLIST AND PROPOSED CLASSIFICATION OF
SYNNEURIDAE AND CANTHYLOSCELIDAE

Family	SYNNEURIDAE Enderlein, 1936
Genus	SYNNEURON Lundström, 1910
	<i>annulipes</i> Lundström, 1910
	<i>decipiens</i> sp. n.
	<i>silvestre</i> Mamaev & Krivosheina, 1969
Genus	EXILISCELIS gen. n.
	<i>californiensis</i> sp. n.
Family	CANTHYLOSCELIDAE Rodendorf, 1951
	<i>Corynoscelidae</i> Enderlein, 1912
	<i>Hyperoscelidae</i> Hardy & Nagatomi, 1960

- Genus **HYPEROSCELIS** Hardy & Nagatomi, 1960
Corynoscelis Boheman, 1858
Spiloptera Zetterstedt, 1860
 ?*Eucorynoscelis* Rodendorf, 1951
eximia Boheman, 1858
insignis Hardy & Nagatomi, 1960 **syn. n.**
veternosa Mamaev & Krivosheina, 1969
- Genus **CANTHYLOSCELIS** Edwards, 1922
- Subgenus **ARAUCOSCELIS** Edwards, 1930
Chiliscelis Tollef, 1959
pectinata Edwards, 1930
pictipennis Edwards, 1930
apicata Edwards, 1934 **syn. n.**
valdiviana Tollef, 1959 **syn. n.**
- Subgenus **CANTHYLOSCELIS** Edwards, 1922
antennata Edwards, 1922
nigricoxa Edwards, 1922
balaena sp. n.
claripennis Edwards, 1922

SYSTEMATICS

Synneuridae and Canthyloscelidae, as treated here, consist of four very well differentiated small genera each of which has a limited distribution within the wide distribution of the group as a whole: *Synneuron* with three species and a Holarctic distribution, *Exiliscelis* with one (possibly two) Nearctic species, *Hyperoscelis* with two Palaearctic species and *Canthyloscelis* with two well marked subgenera, one with two species in the Neotropical region and one with four species in New Zealand. This is strong evidence of a relict group. They are undoubtedly related to the Scatopsidae, which is a relatively large family with a worldwide distribution and about 200 species. Some Scatopsidae, particularly *Coboldia fuscipes* (Meigen), but also such species as *Scatopse notata* (Linnaeus) and *Holoplagia guamensis* Johannsen, have been able to occupy niches over a wide distribution, both naturally and with the aid of man. The Scatopsidae, Synneuridae and Canthyloscelidae are clearly derived from the same stock, the Scatopsidae being the present day successful and versatile lineage.

The evolution of this group and the relationships of one successful group to four relict groups is of interest. In preparing the description of *Exiliscelis*, the Synneuridae and Canthyloscelidae were compared with a variety of Scatopsidae, particularly *Scatopse notata* (Linnaeus), *Aspistes berlinensis* (Meigen), *Anapausis soluta* (Loew), *Psectroscliara africana* Cook and *Ectactia clavipes* (Loew). From this it was apparent that the Scatopsidae and *Synneuron* were almost as closely related to each other as *Hyperoscelis* is to *Canthyloscelis*. *Exiliscelis* appeared to be the most primitive genus and was more closely related to *Synneuron* than to *Hyperoscelis*. A systematic analysis of about 30 characters was prepared, dividing the various states of each character into plesiomorphic (primitive) or apomorphic (derived) condition (Hennig, 1966b) based on the assumption that the whole group belongs to the Mycetophiloid complex of Nematocera. These characters are

TABLE I
Character matrix for 32 characters listed in Appendix I

	32	28	15	13	4	29	2	12	11	16	8	1	14	22	30	5	10	3	26	24	7	9	25	31	19	18	27	17	23	6	20	1	
Scatopsidae	(0)	0	0	(0)	0	(0)	(0)	(X)	X	X	X	X	X	X	0	0	(0)	(X)	X	X	(X)	(X)	(X)	X	X	X	X	X	X	X	X	(X)	(X)
Synneuron	0	0	0	0	0	X	X	0	0	X	X	0	X	X	0	0	X	X	X	X	X	X	X	X	X	0	0	0	0	0	0	0	0
Exiliscelis	0	0	0	0	X	X	X	0	0	0	0	0	0	0	X	X	X	0	X	X	X	X	X	0	0	0	0	0	0	0	0	0	0
Hyperoscelis	0	0	0	X	X	X	X	X	X	X	X	X	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Canthyl- scelis (Arauco- scelis)	0	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Canthyl- scelis (Canthyl- scelis)	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

(X = apomorphic; 0 = plesiomorphic; parentheses indicate that there is some variation.)

listed in the Appendix, giving the state of each character exhibited by the Scatopsidae, followed by the alternative state in square brackets. Where the state is considered to be apomorphic it is given in *italics>*. These can be compared with the descriptions given earlier in this paper. As might be expected in a group containing 200 species, Scatopsidae shows much more variation than in any of the other genera. This may have led to confusion in the selection of the apomorphic state of characters, but it is to be hoped that mistakes of this type have not distorted the overall picture of relationships.

Table 1 shows a character matrix for the 32 characters examined. A representation of the probable phylogenetic relationships based on these data is given in Text-fig. 26 and this agrees with the opinion on relationships arrived at by traditional means.

By both methods the Scatopsidae are only a part of the Synneurid complex and whether the Synneuridae can continue to be maintained as a separate family must be questioned.

Further evidence may exist in the fossil record. Rodendorf (1946) described *Protoscatopse jurassica* from Jurassic material from Kara Tau, Kazakhstan, U.S.S.R. He puts it in a separate family, the Protoscatopsidae. It has not been examined in the present study, but it is obviously a specimen that should be re-examined, since Rodendorf's figures suggest some interesting characters, such as the presence of R_4

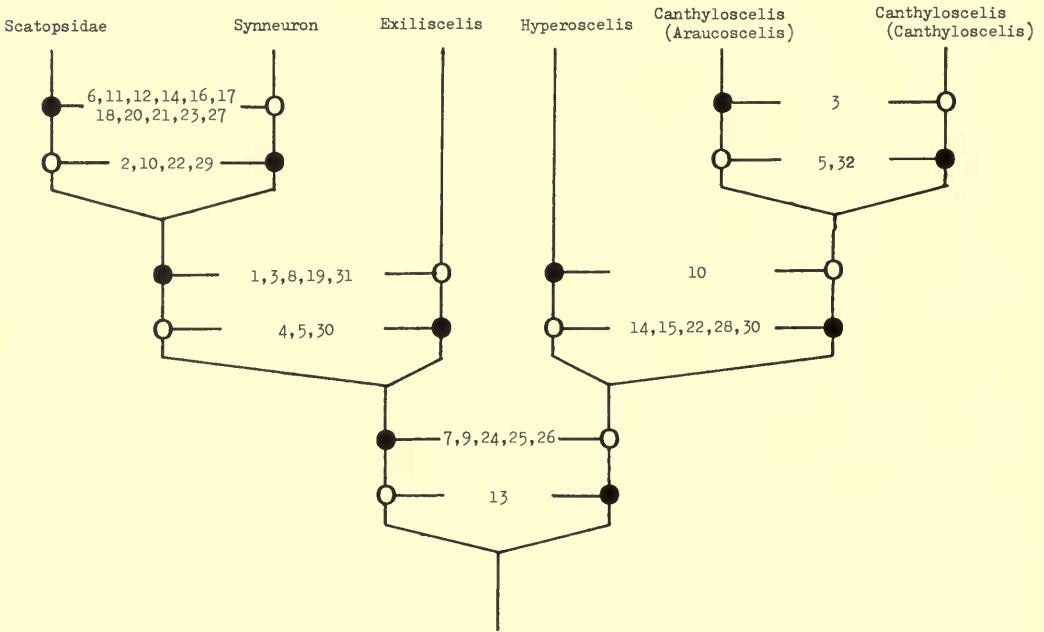


FIG. 26. Phylogenetic relationships of Scatopsidae, Synneuridae and Canthylloscelidae. Numbers refer to the characters listed in Appendix 1 and tabulated in Table 1. ● = apomorphy, ○ = plesiomorphy.

TABLE 2
Comparison of the larval characters of *Canthylloscelis*, *Scatopse*, Mycetophilidae and Cecidomyiidae.

<i>Canthylloscelis</i>	<i>Scatopse</i>	Mycetophilidae	Cecidomyiidae
Head capsule absent	Distinct head capsule	Distinct head capsule	Head capsule very small, but distinct
Near atrophy of mouthparts	Mouth parts well developed	Mouth parts well developed	Mouthparts very reduced
Body of eleven segments	Body of twelve segments	Body of twelve segments	Body of twelve segments
Integument soft, thin and colourless	Integument tough, strongly discoloured with strong hairs and granulations	Integument soft, colourless and usually thin	Integument soft, thin and colourless
Body subcylindrical	Body flattened dorso-ventrally	Body (usually) subcylindrical	Body usually slightly flattened dorso-ventrally
Spiracles sessile	Spiracles on short tubes	Spiracles sessile	Spiracles not or only slightly projecting from body
All spiracles same size and structure	Last pair of spiracles at end of long strong horns	Spiracle 1 larger than others	All spiracles same size
9 pairs of spiracles	9 pairs of spiracles	8 pairs of spiracles	9 pairs of spiracles
Last pair of spiracles on terminal segment of body	Last pair of spiracles on posterior border of penultimate segment	Last pair of spiracles on 7th abdominal segment	Last pair of spiracles on penultimate segment
Terminal armature of two heavily sclerotised horns on single adanal plate	Terminal armature of two soft processes on two isolated plates	Soft terminal lobes sometimes present	Soft terminal lobes sometimes present

A decision on the status given to these groups will eventually have to take note of the recent work on the immature stages.

EVIDENCE OF THE IMMATURE STAGES. The larva of *Canthyloscelis* was described by Tonnoir (1927b) and those of *Synneuron* and *Hyperoscelis* were more recently described by Krivosheina and Mamaev (1967), Krivosheina (1969) and Mamaev & Krivosheina (1969). The larvae are all similar to each other and quite distinct from known Scatopsidae. In describing the larva and pupa of *Canthyloscelis*, Tonnoir (op. cit.) listed differences between this and the larvae and pupae of Scatopsidae, Bibionidae and Cecidomyiidae. A modified summary of this, with the addition of Mycetophilidae and the exception of Bibionidae, is presented in Table 2. The Bibionidae are excepted since they are no longer regarded as a part of the Mycetophiloid complex (although the latter has been regarded as a part of the Bibiomorpha).

The most obvious feature of the larvae of *Synneuron*, *Hyperoscelis* and *Canthyloscelis* is the loss of the head capsule. The description and figures of the larvae of *Synneuron* and *Hyperoscelis* show them to have nine abdominal segments, while there are only eight in *Canthyloscelis* according to Tonnoir (1927b), but it is unlikely that they would differ in such a fundamental character, whilst possessing so much in common. Their shared characters are: the reduction of the head capsule to a weakly sclerotized cephalic plate with very similar antennae and an associated 'enigmatic' organ (Tonnoir, 1927b); the mouth opening and associated internal structures; the sessile spiracles on prothorax and eight abdominal segments, those on the prothorax and last abdominal segments being associated with a sclerotized plate; the soft thin integument with spinulose areas on the anterior region of the dorsal and ventral surfaces of the meso- and metathoracic segments and first six abdominal segments (locomotory aids); the possession of a pair of heavily sclerotized hooks set on a single adanal plate. *Synneuron* and *Hyperoscelis* show slightly greater development of the head than *Canthyloscelis* and there are other differences believed to be of generic significance (Krivosheina, 1969).

Additional information on the larvae of *Scatopse* is given in papers such as those of Morris (1918), Lyall (1929), Bovien (1935), etc. Tonnoir (1927a) described the larva and pupa of *Scatopse subnitens* Verrall (now considered a species of *Rhexosa*) and this is of the same basic pattern as *Scatopse*. The larva of *Ectaetia platyscelis* Loew, described by Laurence (1953), differs from the others in that the spiracles are sessile, the surface ornamentation of the body is much less conspicuous and there is a well developed adanal plate posterior and ventral to the posterior spiracles. In these respects, *Ectaetia* is reminiscent of *Synneuron* and Canthyloscelidae. Mamaev & Krivosheina (1965) have described the larvae of a wide range of genera of Cecidomyiidae, but although there are several features by which they superficially resemble *Synneuron* and Canthyloscelidae, notably the reduction of the head capsule, these similarities must be regarded as the product of convergence. The larvae of the large family Mycetophilidae show considerable variation, but still conform to the basic pattern; the literature is scattered, but papers such as Madwar (1937) and Plassmann (1972) contain a range of species.

The larvae of *Synneuron* and Canthyloscelidae differ from Scatopsidae in other

respects too. The larvae of the former live deep in rotting wood, while Scatopsidae feed in a range of decomposing vegetable and animal matter and may be predaceous. Most of the work on immature stages has been done on *Hyperoscelis*, but it is likely that the similarities in appearance are coupled with similarities in other aspects. Thus the loss of the head capsule is associated with a change to external digestion and there are associated changes in the alimentary canal to the extent that these larvae complete digestion without defecation during the growing period. The larvae of Scatopsidae have well developed mandibles and internal digestion resulting in defecation (Krivosheina, 1969). The larvae of Scatopsidae have a metapneustic first instar, amphipneustic second instar and peripneustic third and fourth instar, while *Hyperoscelis* is peripneustic throughout (Rodendorf, 1964). The nerve chord of *Hyperoscelis* and *Synneuron* consists of the normal number of ganglia, but the cord is contracted and the first abdominal ganglion is displaced into the third thoracic segment (Krivosheina, 1969). Thus the larvae of *Synneuron* and Canthyloscelidae are specialized, while the larvae of Scatopsidae are generalized.

This situation begins to reverse in the pupal stage since in Scatopsidae the last larval skin is retained as a primitive puparium, which is absent in the others.

RESULTS. The immature stages of the Scatopsidae are quite distinct from those of the three genera *Synneuron*, *Canthyloscelis* and *Hyperoscelis*. On the other hand, the adults do not show the same division. Most of the major differences in the larvae are obviously derived from a single feature, namely the specialized feeding habit of *Synneuron* and Canthyloscelidae, but to conform to the plan of evolution expressed in Text-fig. 26 this habit must have arisen at least twice: once for the Canthyloscelid lineage and once for *Synneuron*. If *Exiliscelis* really is an older relict than the others, the discovery of its larva would be most valuable in adding to the picture. It is possible that the modifications of the larva is the means whereby this group of relicts has been able to survive.

In the absence of data on the larva of *Exiliscelis* the larval characters were not included in the phylogenetic analysis, but assuming that these characters are the product of a single apomorphy, it is unlikely to change the overall picture very much. There is ample justification on the basis of adult morphology for separating the Synneuridae and Canthyloscelidae, but if one were to accept the full force of Hennig's (1966b) argument, it would not be possible to separate the Synneuridae (*Synneuron* and *Exiliscelis*) from the Scatopsidae. An evolutionary classification based on the time of common ancestry would have to place Scatopsidae and *Synneuron* in the same taxon or as equivalently ranked taxa. However, the Scatopsidae are a compact and easily definable group that has apparently evolved much more rapidly and successfully than the other groups under discussion and so for convenience of classification and because of differences in their biology and evolutionary success, I prefer to retain the Synneuridae and Scatopsidae as separate families.

ZOOGEOGRAPHY

Hennig (1966a) used *Hyperoscelis* and *Canthyloscelis* as an example to discuss the possible routes of origin of Australasian/South American faunal relationships. He did not include *Synneuron* in this discussion. I regard the new genus, *Exiliscelis*,

as an evolutionary link between *Synneuron* and *Hyperoscelis/Canthylloscelis* and one that should be considered in any discussion on the routes of origin of the group. While the occurrence of the new genus in the Nearctic region cannot eliminate any of the possible routes suggested, it may offer an opportunity to extend the discussion and increase the probability of certain routes.

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APPENDIX: LIST OF CHARACTERS INVESTIGATED FOR
PHYLOGENETIC ANALYSIS

The character investigated is followed by a statement as to the state of this character exhibited in the Scatopsidae. This is followed, in square brackets, by the alternative state. The state considered to be apomorphic is given in italics. The character state for the various Synneuridae and Canthyloscelidae can be found in the earlier text of this paper and all these data are summarized in the character matrix diagram (Text-fig. 26).

1. Head shape. *Rounded and somewhat flattened*. [Longer than broad.]
2. Ocelli. Three small equally spaced (except in Psectrosciarinae, in which *median ocellus is smaller*). [*Median ocellus reduced or absent*.]

3. Eyes. *Meet over antennae* (except in *Lumpuria*, ♀ *Colobostema* and *Aspistinae*), well separated below. [Narrowly separated above antennae.]
4. Antennae. *7-12 short closely jointed segments* covered with small setae and whorls of rather larger setae (except in *Lumpuria*, in which flagellar segments are quite long and the 10-segmented antennae are at least as long as the head and thorax). [16-segmented antennae.]
5. Gena. Not developed (except in *Swammerdamella*). [Well developed.]
6. Mouthparts. *1-segmented maxillary palp*, 1 median or small pair of cradostipites, proboscis with prominent labellae (single pseudotrachea in *Ectaetia* only). [4-segmented palps, labellae prominent or inconspicuous.]
7. Thorax shape. *Elongate and laterally compressed* (not so much in genera such as *Holoplagia*, *Colobostema* and *Parascatopse* (Scatopsinae), *Lumpuria* and *Aspistinae*; very narrow and elongate in *Psectrosiara*). [Stoutly developed.]
8. Prothorax. *Stoutly developed*. [Reduced but forming a distinct collar.]
9. Anterior spiracle. *On separate sclerite* in Scatopsinae and *Lumpuria*. On anepisternite in others, but *partly separated* in Psectrosiarinae and Ectaetiinae. [On anepisternite.]
10. Sternopleuron and meron. Sternopleuron only slightly larger than meron in Scatopsinae (better developed and meron less well developed in *Aspistinae*, Ectaetiinae and Psectrosiarinae respectively). [*Sternopleuron prominent, meron very small.*]
11. Scutellum. *Well developed and prominent*. [Poorly developed, not prominent.]
12. Fore coxae. *Short* (long in *Psectrosiara*, also in Ectaetiinae and *Aspistinae*). [Long.]
13. Legs. Unremarkable (Tibia sometimes modified, e.g. *Aspistes*). [*Swollen hind femora, tibia curved to fit femur.*]
14. Tibial spurs. *True spurs ? not present*, usually a weak tibial comb, sometimes suggestive of spurs. [*Well developed comb* or distinct spurs present.]
15. Tarsal claws. Simple. [*Large basal lobe with small teeth.*]
16. Empodium. *Large and setaceous*. [Narrow, fringed.]
17. Wings. *Short and broad with well developed anal lobe*. [Longer and narrow, anal lobe absent.]
18. Wing vein pigmentation. *Costa, radius and base of media pigmented, rest weak*. [Posterior veins well developed and well pigmented.]
19. Vein R_4 . *Absent* [Present or represented by a fusion.]
20. Vein *r-m*. *Absent* (Cross-vein in some *Scatopse* and *Holoplagia* is called *r-m*, but may not be homologous). [Represented by a fusion.]
21. Vein M_1 . Sometimes *interrupted at base*. [Complete.]
22. Vein M_2 . Complete. [*Interrupted at base.*]
23. Vein *m-cu*. *Absent*. [Present or represented by a fusion.]
24. Vein Cu_2 . *Absent*. [Weakly present.]
25. Anal vein. Present or *absent*.
26. Vein *Sc*. *Sometimes weakly present*. [Faint to well developed.]
27. Costa. *Ends at end of R_5* . [Extended beyond end of R_5 .]
28. Number of unmodified pregenital segments. Seven. [*Reduced.*]
29. Male sperm pump. Attached to genital complex in all but Scatopsinae, in which it is *free in abdomen*.
30. Male sperm pump. Not encapsulated. [*Encapsulated.*]
31. Ovipositor. *One-segmented*. [Two-segmented.]
32. Spermatheca. One, simple (*modified* in *Ectaetia*.)

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